

Zonation of molluscan species across the tidal flats of Bahia la Choya (Gulf of California, Sonora, Mexico): Paleoecological significance

By

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With 14 figures in the text

ABSTRACT

In Bahia la Choya, a shallow protected bay in the northern Gulf of California, many of the dominant species of live molluscs exhibit a zonation from shallow subtidal to high intertidal environments. Many dominant species of the taphocoenoses show a corresponding distribution pattern. The pattern is modified mainly by seaward transport of mobile, epifaunal species inhabiting inner flat firmgrounds. The distribution patterns of live and dead molluscs therefore show consider-

able similarity. Limited transport is caused by ebb flow along the tidal channel and by hermit crabs. Time-averaging strongly affects species diversity within the taphocoenoses, but does not significantly alter the distribution pattern of species. If diagenetic distortion of Bahia la Choya shells will remain small, the future fossil assemblages would serve as useful environmental indicators.

KURZFASSUNG

Unter den lebenden Molluskenarten von Bahia la Choya, einer flachen, geschützten Bucht im nördlichen Golf von Kalifornien, weisen die dominierenden Formen eine Zonierung zwischen dem flachen Subtidal und dem höheren Intertidal auf. Viele dominierende Arten der Taphozönosen zeigen ein Verteilungsmuster, das weithin mit dem der lebenden Formen identisch ist und hauptsächlich durch den seewärtigen Transport von vagilen, epifaunalen Arten aus dem Innenwatt modifiziert ist. Das Verteilungsmuster lebender und toter Ar-

ten ist deshalb ähnlich. Schalentransport findet vor allem durch den Ebbstrom entlang der Gezeitenrinne statt sowie durch Einsiedlerkrebse. Die zeitliche Mittelung von Faunengemeinschaften führt zu einer starken Erhöhung der Diversität in den Taphozönosen, aber nicht zu einer bedeutsamen Änderung des Verteilungsmusters der Arten. Bleiben diagenetische Verzerrungen der Molluskenfauna von Bahia la Choya unbedeutend, so würden die zukünftigen Fossilvereinigungen brauchbare Milieu-Indikatoren darstellen.

INTRODUCTION

The value of fossils for paleoecological or environmental reconstructions depends on how faithfully their present-day distribution reflects their original distribution pattern and on how accurately the composition of fossil assemblages mirrors that of the ancient communities. Several studies address this topic (e. g. ANTIA 1977, CADEE 1968, CARTHEW & BOSENE 1986, JOHNSON 1965, PETERSON 1976, STAFF et al. 1986, WARME 1969, WARME et al. 1976, WILSON 1967), but the results are conflicting. Thus we are far from being able to confidently evaluate the information loss that communities suffer during their transition from live to dead to fossil assemblages.

The aim of the present study is to increase our knowledge of the degree of distortion of benthic molluscan communities. We compare the distribution patterns of live and dead individuals within species. In addition we analyse the distribution of dead individuals along environmental gradients to see how much the distribution corresponds to various subenvironments. We have chosen an environmental setting, the tidal flat, in which this distortion (due to frequent reworking and strong tidal currents) can be expected to be pronounced compared to other, more favorable environments. Surprisingly, our results suggest that even under such unfavorable conditions the degree of distortion is limited and that the distribution of individual species in highly time-averaged death assemblages still correlates with environmental gradients.

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STUDY AREA AND METHODS

Bahia la Choya is a protected bay situated in the northern Gulf of California, about 10 km northwest of Puerto Peñasco (Sonora, Mexico). A tidal range of 7.9 m (THOMSON et al. 1969) exposes (at spring low tide) a predominantly sandy tidal flat of about 10 km² in area (Fig. 1). A detailed description of the tidal flat and various environmental parameters such as salinity, water temperature, precipitation and wind directions can be found in FURSICH et al. (this volume). Bahia la Choya comprises shallow subtidal areas, the tidal flat which can be subdivided into an outer, mid, and inner flat, and an extensive salt marsh. A major tidal channel originates in the salt marsh and drains both marsh and tidal flat. Landward, the tidal flat is bordered by a subrect spit which consists nearly exclusively of shells and shell debris. As is typical of tidal flats there is a decrease in grain size from fine-sand (outer flat) to fine-sandy silt of the inner flat. In the inner flat, the sediment is highly compacted and forms a firmground. Sedimentary structures vary from sand waves (outer flat) to small current ripples (outer to inner flat), megaripples (inner tidal channel), linguoid ripples (small tidal creeks) and current lineation (major tidal channel). Bioturbation occurs throughout the area and is particularly intense in inner flat and salt marsh where the shrimp *Callinassa* and various crabs (*Uca*, *Eurytium*) occur in high densities.

The net rate of sedimentation is very low. Exposures of lithified Pleistocene occur scattered across the tidal flat, particularly in outer flat areas. In the northern part of the study area, sediment frequently forms only a thin veneer of several centimetres on top of Pleistocene rocks, whilst in the southern part sediment thickness may reach more than 1 m. Low sedimentation rates and frequent reworking lead to formation of highly time-averaged shell concentrations (see FEIGE & FURSICH, this volume).

The benthic shelly macrofauna is dominated by molluscs. Echinoids, barnacles, serpulids, and bryozoans form only minor constituents of the fauna.

DISTRIBUTION PATTERNS OF LIVE AND DEAD SPECIES

Distribution patterns of live species give information on how closely the benthic fauna corresponds to environmental gradients. The relative abundance of dead species along these gradients allows us to establish the degree of distortion due to taphonomic processes. Because live individuals of most species were rare, live-dead comparisons had to be restricted to a few common species.

When absolute abundances (expressed by the numbers of individuals) of live and dead species are compared along Transects A and B (Fig. 2), dead individuals are invariably far more abundant than live ones. The highest densities of live individuals occur in channel areas (Transect B), close to exposed Pleistocene rocks and on the inner flat (Transect A). Dead individuals are very abundant in outer to mid flat areas and in the tidal channel. Very low densities are found in the shallow

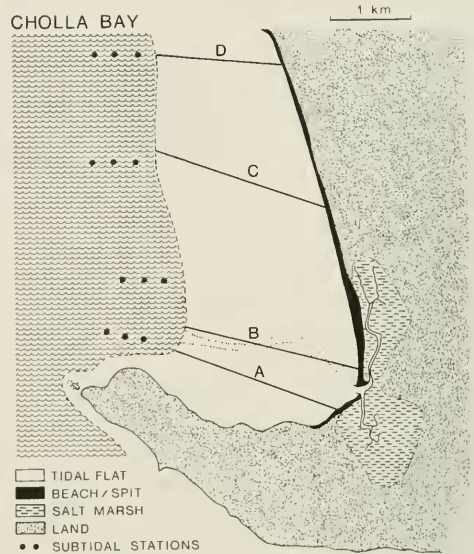


Fig. 1: Map of Bahia la Choya showing location of the four transects (A-D) and the subtidal stations.

Between December 1985 and May 1986 the shelly macrofauna was sampled along four transects at 200 m intervals (shallow subtidal areas) and at 100 m intervals (tidal flat). (For detailed description of sampling methods see FURSICH et al., this volume.) In the laboratory, live and dead faunal elements were treated separately. The molluscs were identified using KEEN (1971), KEEN & COAN (1976) and OLSSON (1961). For each sample, species composition and relative abundance was recorded. In the case of disarticulated bivalves, the larger number of right or left valves was used to indicate the number of specimens present.

subtidal and on the inner flat. The high shell density in the innermost flat at Transect B (Fig. 2b) is due to contamination by shells from the adjacent spit.

The very low shell density of the inner flat is a result of the firm substrate. The firmground of the inner flat prevents rapid burial of shells and facilitates removal by currents. As will be seen below this factor strongly affects the distribution of species in the taphocoenosis. Compared to Transects C and D, which cover the northern part of Bahia la Choya, shells are more abundant in the southern part (covered by Transects A and B; see Fig. 1). This is particularly true of small shells (≤ 1 cm) and can be explained by the more protected position of the southern part of the bay. This corresponds to a generally higher sediment thickness in this area in comparison to the area further north.

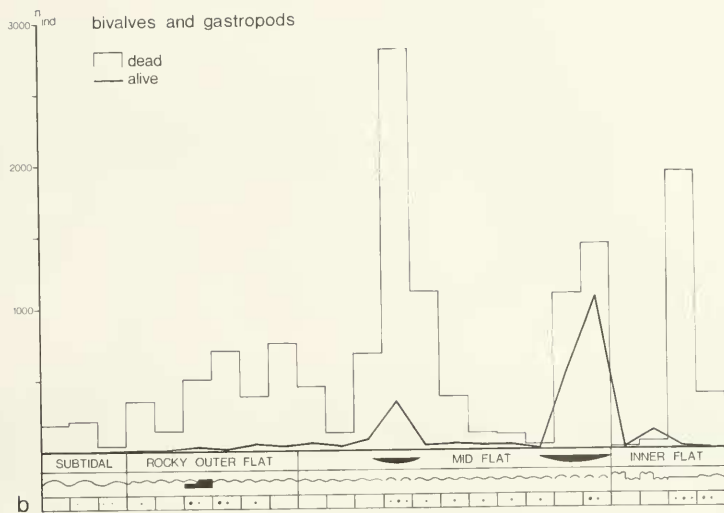


Fig. 2: Distribution of live and dead individuals of gastropods and bivalves along Transects A (a) and B (b). For key see Fig. 3.

In Fig. 3 the numbers of live and dead species along Transects A and B are compared. As one would expect from the discrepancy in numerical abundance of live and dead individuals, there are far fewer live species than dead ones. Whereas species diversity of live molluscs is fairly constant (ranging usually from 5 to 10), up to 71 species are represented in the ta-

phocoenoses, with most samples averaging between 40 to 60 species. Diversity of dead molluscs is considerably lower on the inner flat compared to outer-mid flat areas (with exception of the spit-contaminated innermost part of Transect B). This may partly be due to the low burial potential of faunal elements on inner flat firmgrounds.

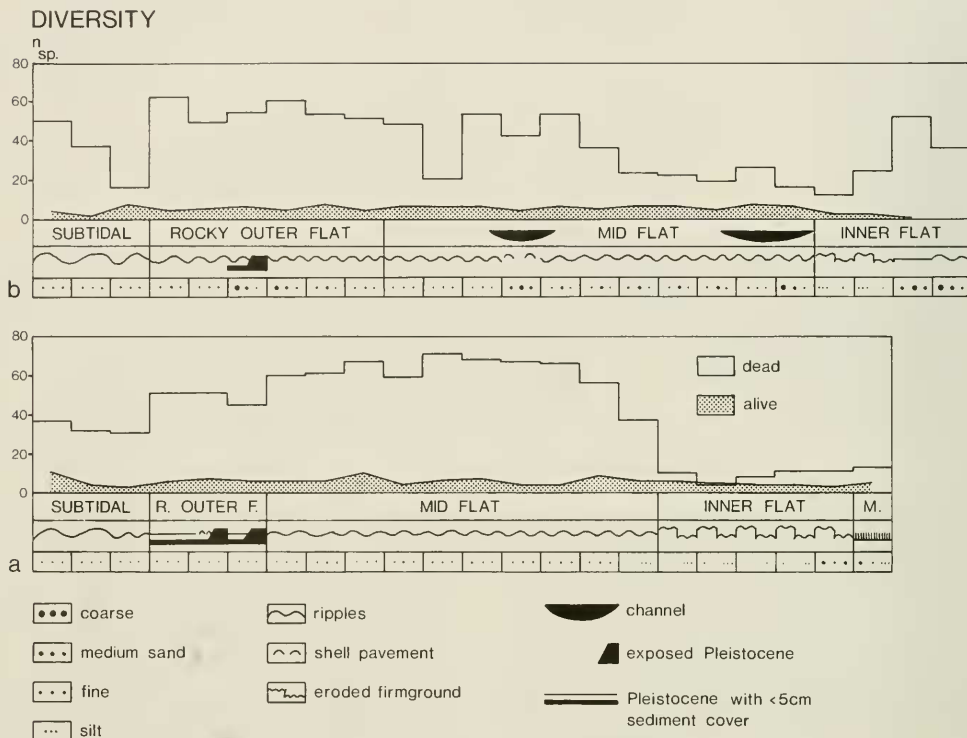


Fig. 3: Variation in the number of live and dead bivalve and gastropod species across the tidal flat.

The considerably higher number of species found only as dead individuals over most part of the tidal flat suggests extensive time-averaging. Diversity of the live fauna at any one time was relatively low: The highest number of live mollusc species recorded during our study was 15 (on rocky outer flats). Fluctuations in larval settling as well as minor environmental fluctuations caused changes in the composition of the benthic molluscan fauna through time. This led to an increase of faunal diversity within the taphocoenoses over time.

Figs 4–9 illustrate the distribution of live and dead individuals of some characteristic species across the tidal flat. Gastropods occur far more commonly alive than do bivalves. Fig. 4 shows the distribution of live and dead *Cerithium stercusmuscarum*, an epifaunal grazing gastropod, along the four transects. Live specimens are most commonly found in the channel (Transect B) and on exposed Pleistocene rocks (Transects A, C, D). Dead specimens show a very similar distribution pattern and occur only in very low numbers out-

side the range of live specimens. Live *Cerithium* are sometimes far more abundant than dead ones which suggests local redistribution of empty shells by currents or biological agents. Distribution of live *C. stercusmuscarum* is not related to any environmental gradients of the tidal flat as they occur from subtidal to high intertidal areas. Rather, they are substrate related, preferring hard substrate (Pleistocene rock of the tidal flat and gravel within the main channel) where their food source is most abundant. The distribution of live *C. stercusmuscarum* is slightly modified, after death, by waves and currents which sweep the shells from hard substrates onto the surrounding sandy flat. In addition, biological transport is probably also very important as *Cerithium* shells are frequently inhabited by hermit crabs.

Live specimens of *Cerithidea mazatlanica* (Fig. 5), an epifaunal detritus-feeder, occur predominantly on inner flat firmgrounds and in the salt marsh. They are therefore restricted to the southern part of Bahia la Choya where these suben-

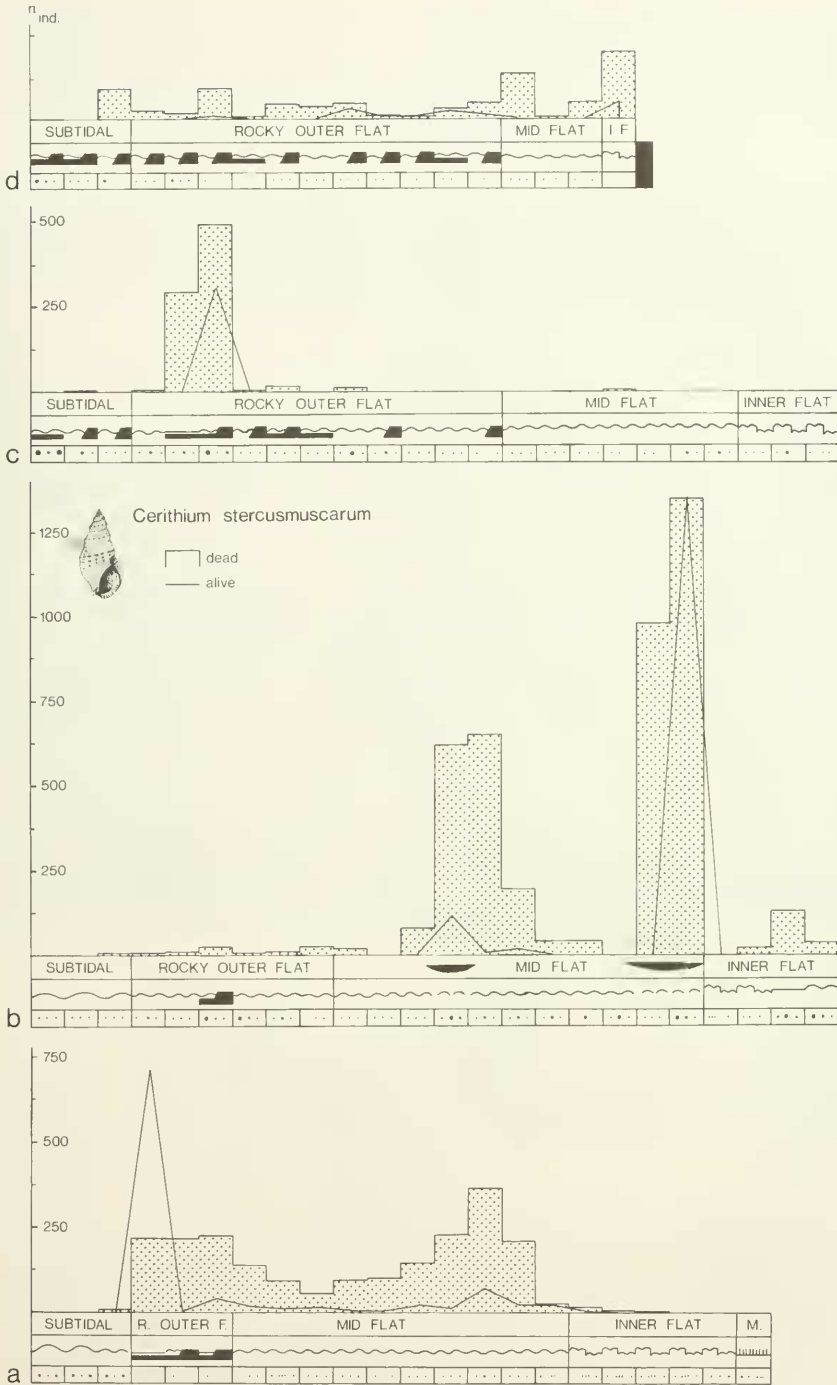


Fig. 4: Distribution of live and dead individuals of the gastropod *Cerithium stercusmuscarum* across the tidal flat. a-d: Transects A-D. For key see Fig. 3.



Cerithidea mazatlanica

□ dead
— alive

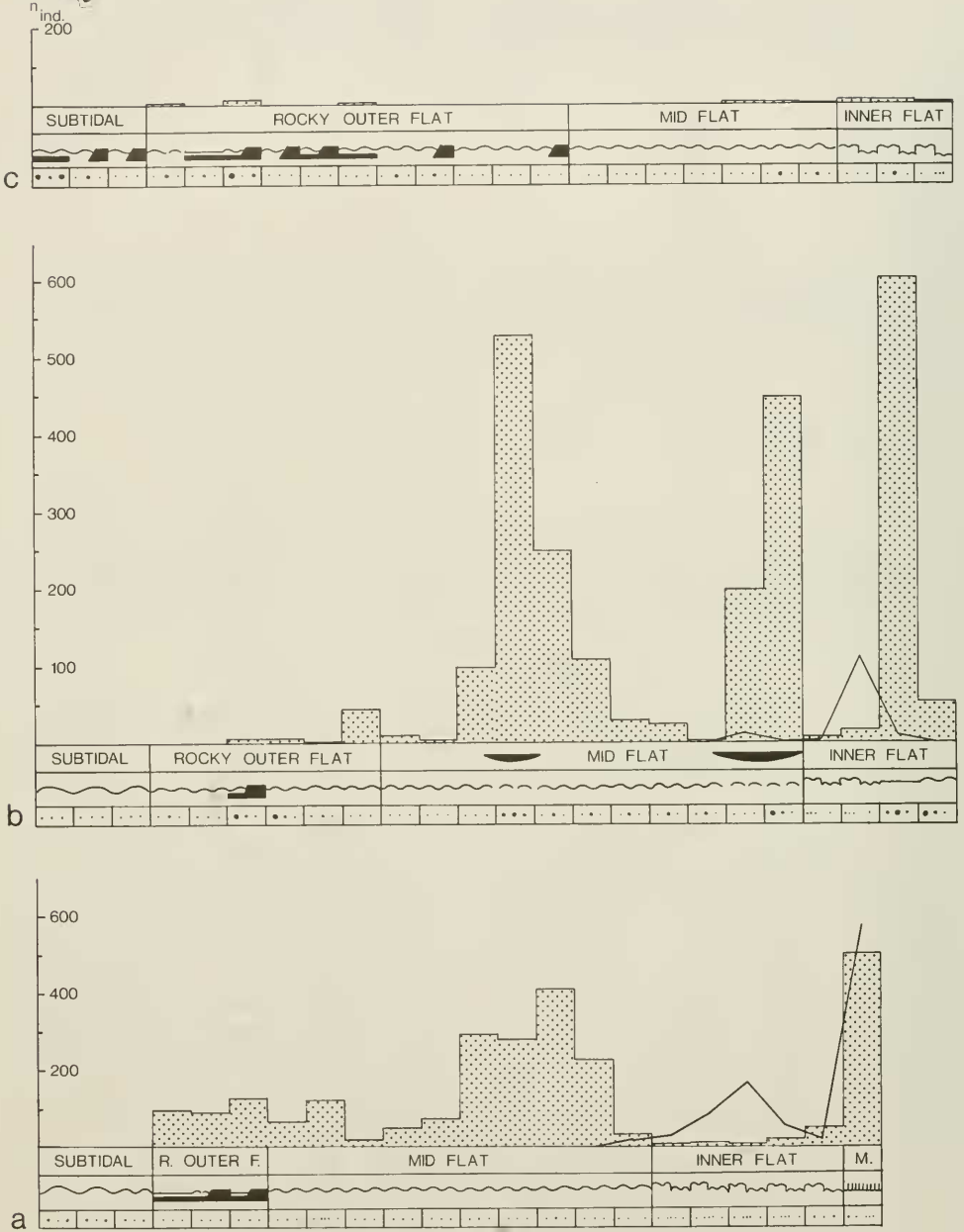


Fig. 5: Distribution of live and dead individuals of the gastropod *Cerithidea mazatlanica* across the tidal flat. a-d: Transects A-D. For key see Fig. 3.

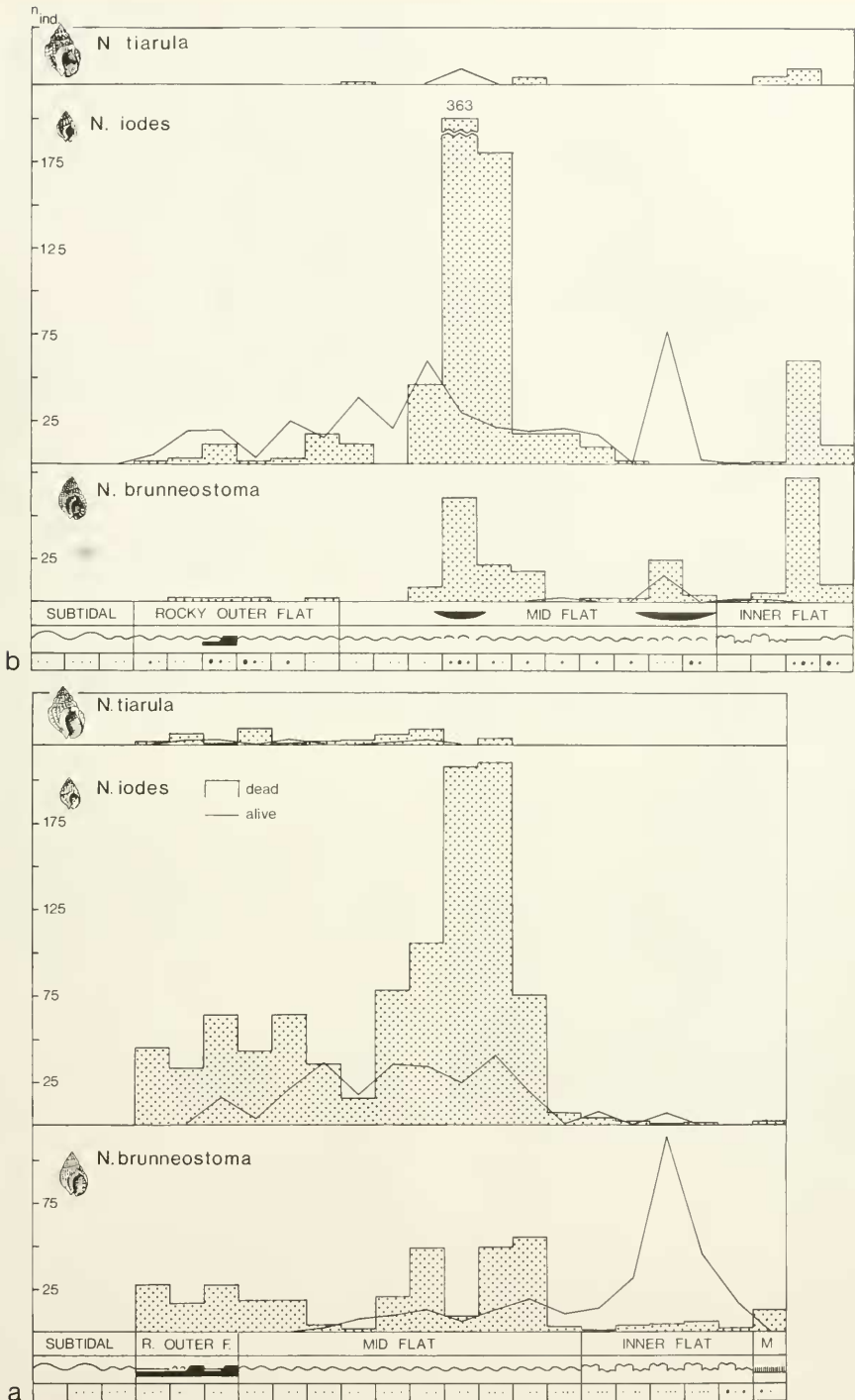


Fig. 6: Distribution of live and dead individuals of species of the gastropod *Nasarius* across the tidal flat. a: Transect A; b: Transect B; c: Transect C; d: Transect D. For key see Fig. 3.

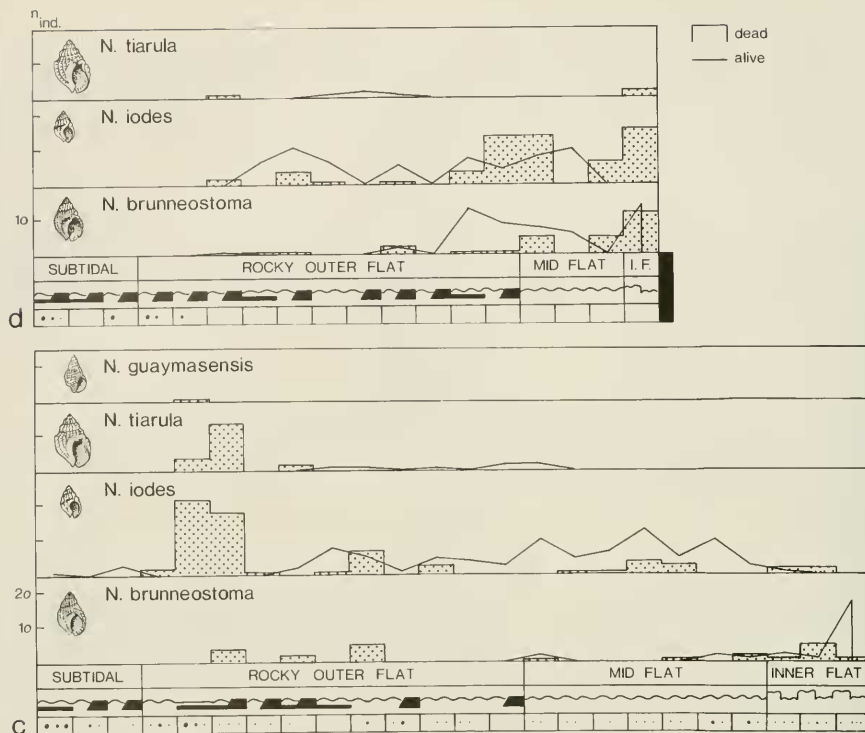


Fig. 6 (cont.)

vironments cover large areas. Dead individuals are found abundantly in marsh, channel and outer to midflat areas of Transects A and B, rarely in Transect C and not at all in D.

Comparison of live-dead distribution patterns show that dead specimens are more widely distributed than live ones and that they do not precisely correspond to each other except in the salt marsh. Clearly, dead individuals are swept off the inner flat firmground with its low burial potential, become concentrated in the channel (Transect B) and are moved seaward. This seaward transport is also seen in Transect A. Specimens in mid to outer flat areas, however, differ strongly in their preservation quality from those of inner flat and marsh areas. In the inner flat and marsh areas well and poorly preserved specimens occur together, whilst in the former only highly abraded and bioeroded shells are found. As with *Cerithium*, hermit crabs commonly inhabit dead *C. mazatlanica* shells and cause biological transport, also in a seaward direction. In contrast to this marked offshore transport, there is hardly any transport parallel to the shoreline, as is indicated by the scarcity of *C. mazatlanica* in Transects C and D. Specimens from the spit cause the peak of dead individuals on the innermost flat of Transect B. These specimens can be easily recognized as reworked because they have a different surface texture and obviously have experienced a different taphonomic history.

Three species of the epifaunal scavenger *Nassarius* (*N. brunneostoma*, *N. iodes*, *N. tiarula*) occur in Bahia la

Choya. A fourth species, *N. guaymasensis* is found only in the taphocoenosis. The live species show a rough zonation across the tidal flat (Fig. 6): *N. tiarula* occurs, albeit in low numbers, mainly in outer to midflat areas as does the very abundant *N. iodes*. The latter, however, has its peak distribution in the midflat. *N. brunneostoma*, in turn, dominates inner flat firmgrounds and less commonly extends its range to midflat areas (e. g. Transect A).

In the taphocoenosis, the rare *N. guaymasensis* is restricted to subtidal and outermost flat areas, *N. tiarula* occurs from outer to midflat with a somewhat higher abundance in the former, and *N. iodes* is very widely distributed, its range extending across the whole intertidal flat. *N. brunneostoma* likewise is found from outer to inner flat and shows a high concentration in the channel.

Comparing live-dead distribution patterns leads to mixed results: Whilst the distribution of dead *N. tiarula* mirrors that of live ones and live and dead *N. iodes* show a roughly similar distribution, this is not the case with *N. brunneostoma*. Again, it is the low burial potential of individuals living on inner flat firmgrounds, in combination with tidal currents and hermit crab activity, which leads to their dispersal across a wide area and thus to a distortion of their original distribution pattern. The rough zonation of live species of *Nassarius* across the tidal flat cannot be recognised in the taphocoenosis.

Fig. 7 records the distribution of live and dead *Theodoxus luteofasciatus*, an epifaunal algal scraper. Live individuals oc-

cur most abundantly in the channel (Transect B), but are also found on exposed Pleistocene rocks from outer to inner flat areas (Transects A, D). *T. luteofasciatus* therefore shows a very strong relation to hard substrates. For example, the species is frequently found sitting on *Cerithium stercusmuscarum*, especially in the tidal channel. The distribution of dead individuals closely correlates with that of live ones and apparently little transport takes place after the animals die. This is surprising as in their favorite habitat, the tidal channel,

current velocities are high (values between 0.5 and 1.2 m/sec. were recorded during ebb flow). However, the taphonomic history of *T. luteofasciatus* may explain this discrepancy: After death, *Theodoxus* shells quickly become abraded and bioeroded. As the shells are fairly thin they are easily fragmented and, during longer transport, destroyed. The poor durability of the shells therefore prevents distortion of the original distribution pattern despite the presence of strong currents.

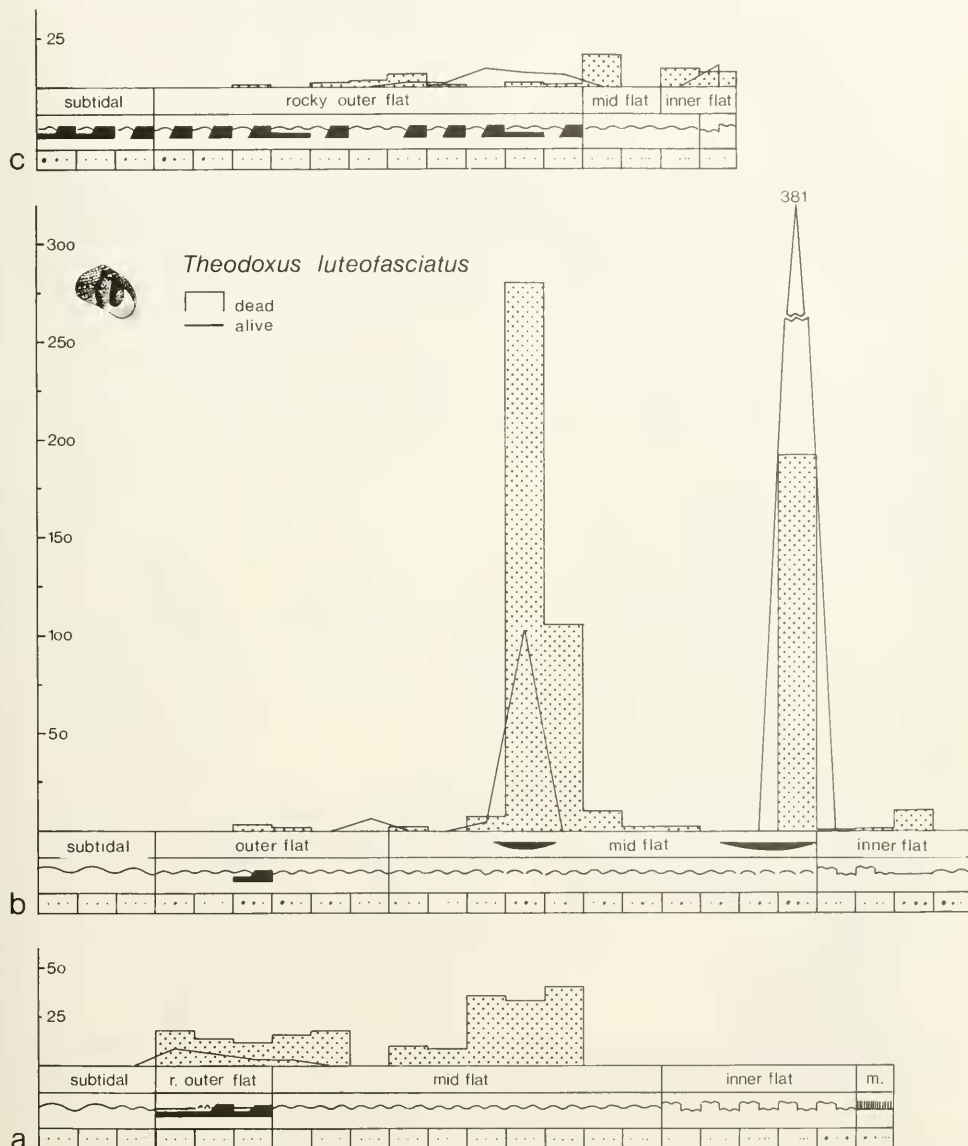


Fig. 7: Distribution of live and dead individuals of the gastropod *Theodoxus luteofasciatus* across the tidal flat. a: Transect A; b: Transect B; c: Transect D. For key see Fig. 3.

Only in the case of *Protothaca grata* and *Donax navicula* are live bivalves abundant enough to allow comparison with their dead counterparts. Live *Protothaca grata*, a shallow burrowing suspension-feeder, occur among pebbles along the southern shore of Bahía la Choya. Across the tidal flat they are rare except along Transect B where they are found in gravelly sediments of the inner channel and, more rarely, on the surrounding sandy flat (Fig. 8). Dead individuals have a much

wider distribution, occurring from the inner channel to the outer flat. (Their presence in innermost flat areas is again due to contamination by material from the spit.) This pattern clearly records transport of shells along the channel in a seaward direction. However, transport affects only the small shells whereas large individuals of dead *P. grata* occur only where living specimens are found.

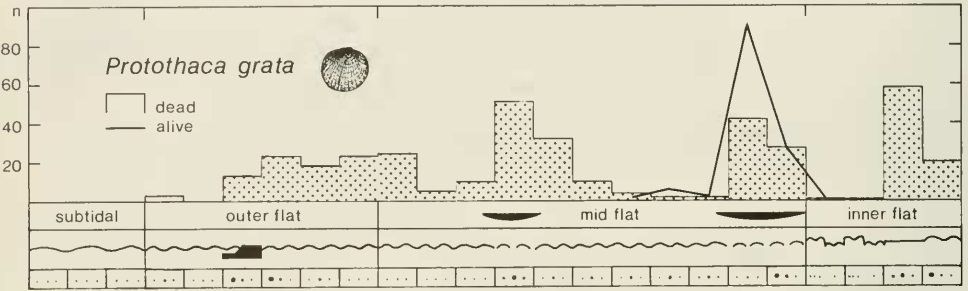


Fig. 8: Distribution of live and dead individuals of the bivalve *Protothaca grata* across the tidal flat (Transect B). For key see Fig. 3.

Live specimens of the shallow burrowing suspension-feeding bivalve *Donax navicula* occur scattered across outer to midflat areas (Fig. 9). Dead individuals exhibit an identical di-

tribution pattern (if one neglects recycled specimens from the spit introduced into nearshore areas).

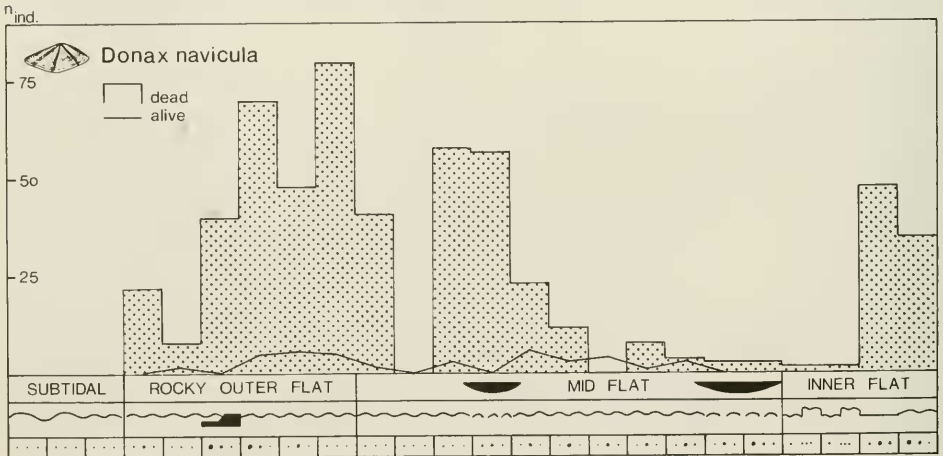


Fig. 9: Distribution of live and dead individuals of the bivalve *Donax navicula* across the tidal flat (Transect B). For key see Fig. 3.

DISTRIBUTION PATTERNS OF THE MOST COMMON SPECIES ACROSS THE TIDAL FLAT

Figs. 10–13 illustrate the distribution patterns of the most common molluscan species of the taphocoenoses from shallow subtidal areas to the salt marsh. In contrast to the live-

dead comparisons (which were given in absolute numbers), relative abundances of individual species are given.

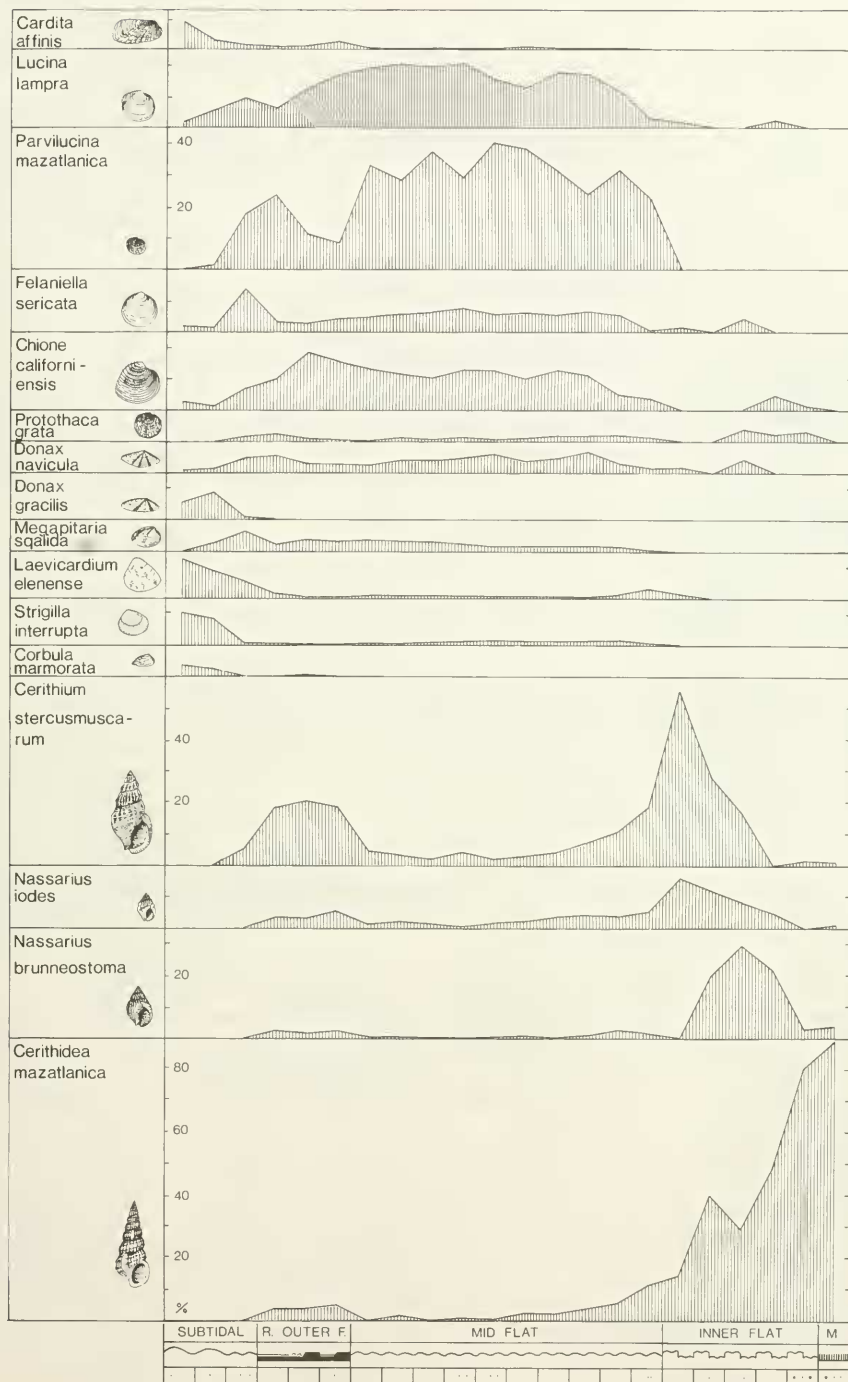


Fig. 10: Distribution of common species of the taphocoenoses across the tidal flat (Transect A). For key see Fig. 3.

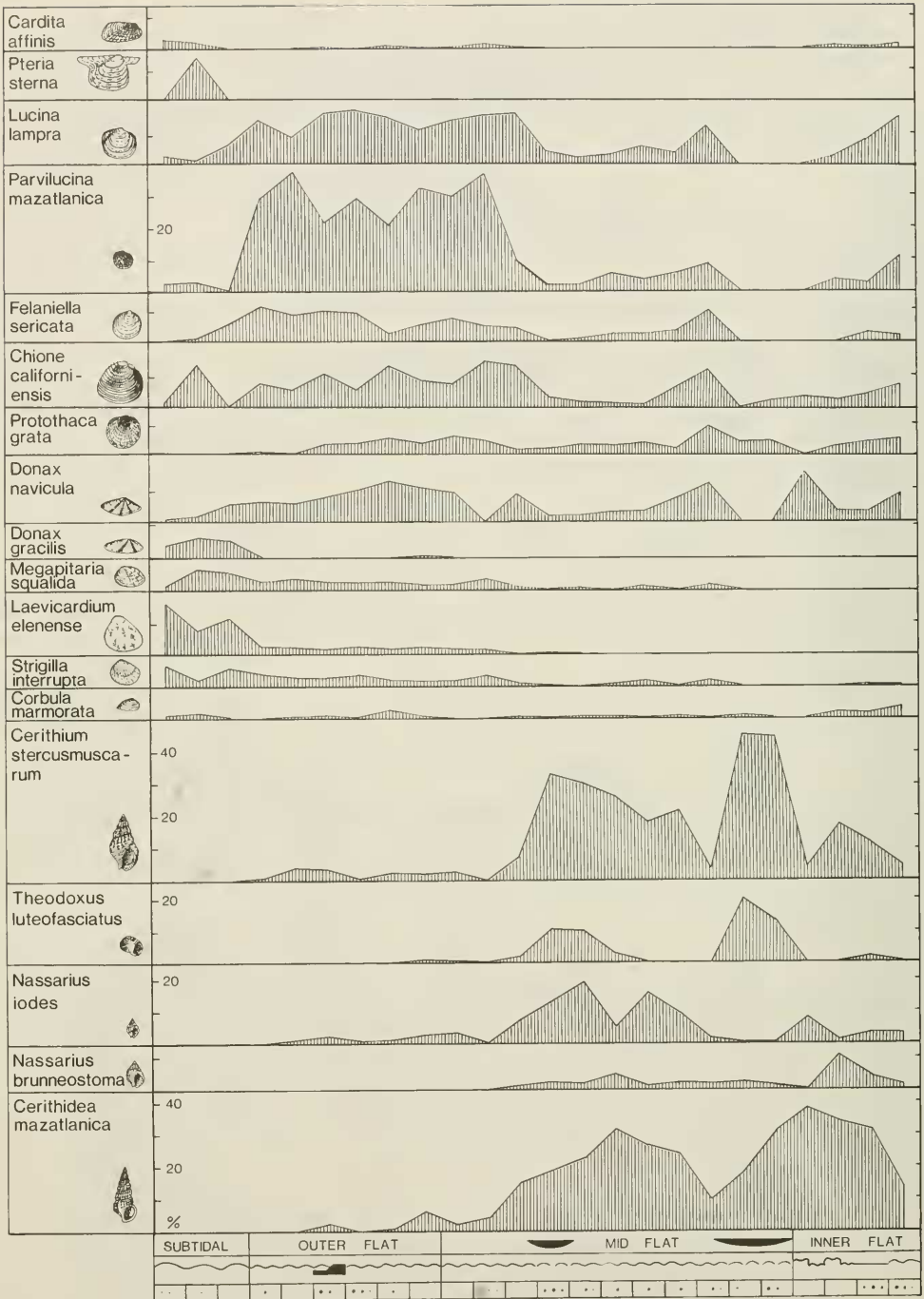


Fig. 11: Distribution of common species of the taphocoenoses across the tidal flat (Transect B). For key see Fig. 3.

Transects A and B from the southern part of the bay record a typical tidal flat sequence extending from shallow subtidal to marsh environments. Each subenvironment is relatively

well defined. Correspondingly many species show a characteristic distribution pattern (Figs 10–11). For example, subtidal areas are characterized by the bivalves *Laevicardium ele-*

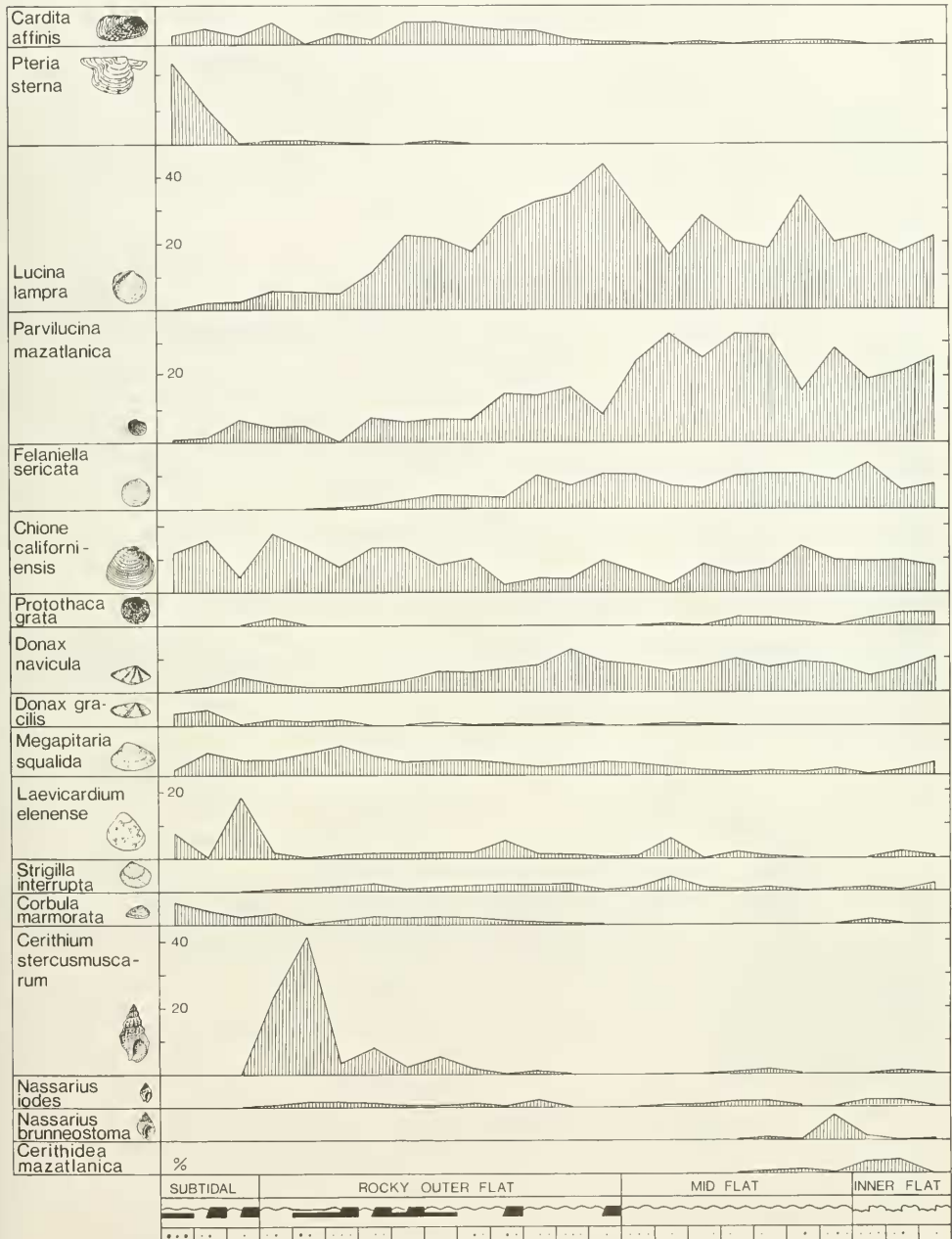


Fig. 12: Distribution of common species of the taphocoenoses across the tidal flat (Transect C). For key see Fig. 3.

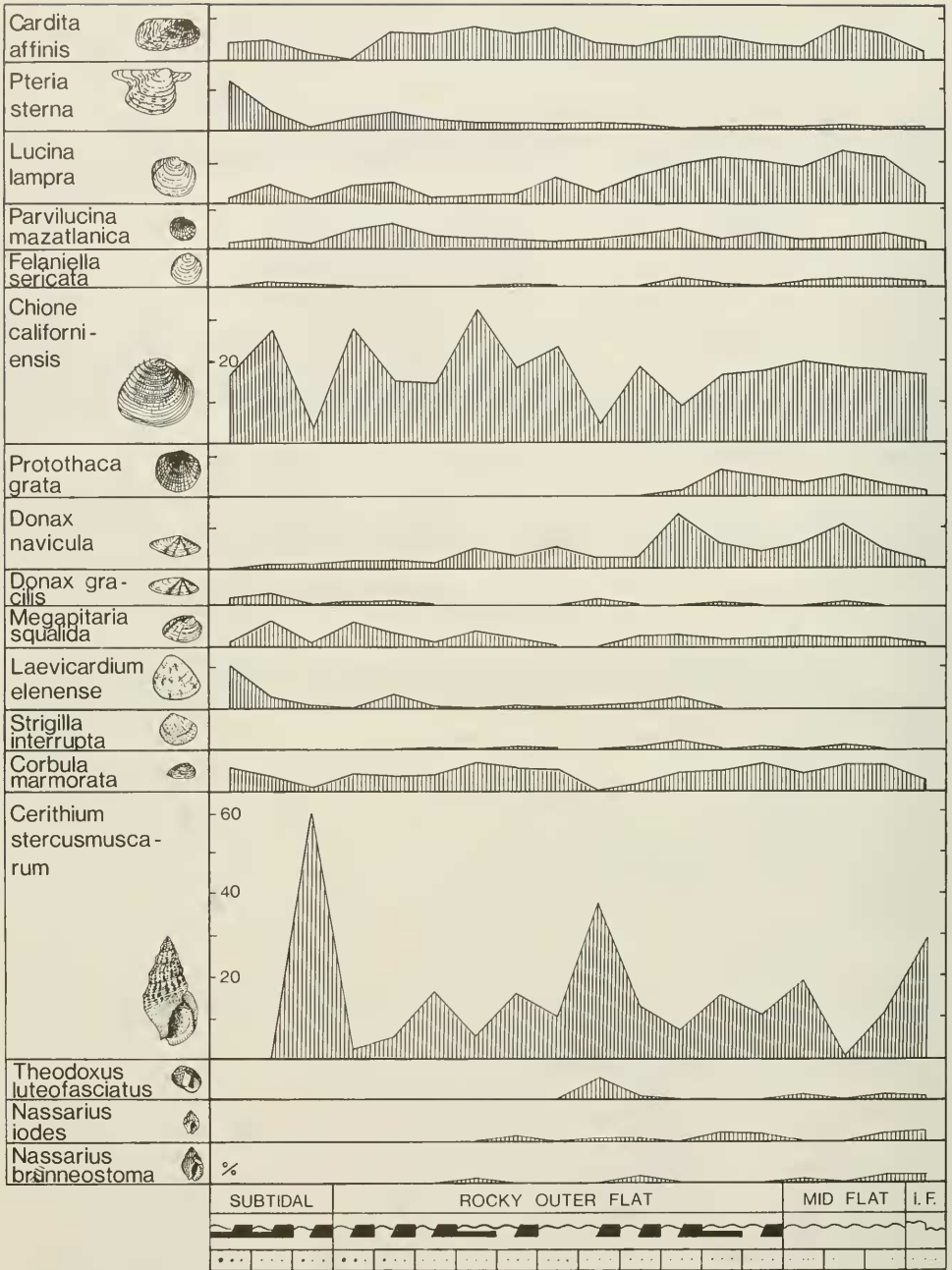


Fig. 13: Distribution of common species of the taphocoenoses across the tidal flat (Transect D). For key see Fig. 3.

nense, *Donax gracilis*, *Cardita affinis*, *Strigilla interrupta*, *Pteria sterna* and *Corbula marmorata*. Outer to mid flat areas are dominated by small lucinid bivalves (*Parvilucina mazatlanica*, *Lucina lanpra*, *Felaniella sericata*) and *Megapitaria squalida*. On inner flat firmgrounds gastropods dominate (*Cerithidea mazatlanica*, *Nassarius brunneostoma*). In the channel, *Cerithium stercusmuscarum* and *Theodoxus luteofasciatus* are abundant. The former also occurs on exposed Pleistocene rocky substrates and on inner flat areas. Several species are not restricted to one or two of the subenvironments, but occur across the whole tidal flat. They include *Chione californiensis*, *Donax navicula*, *Nassarius iodes* and *Felaniella sericata*. In Transect B, the pattern is slightly modified by shells that wash out from the neighboring spit and accumulate nearshore.

Transects A and B show that the distribution patterns are governed not only by parameters which change in an onshore-offshore direction, but are also related to the presence of hard substrate. Hard substrates crop out patchily in the southern part of Bahía la Choya and become very abundant towards the north. This is reflected by the faunal distribution along Transects C and D where only few trends are seen and the presence or absence of hard substrate seems to exert a major role on the distribution of the mollusc fauna (Figs 12–13).

DISCUSSION

ZONATION OF LIVE FAUNA

Even with the few data presented in Figs 4–9 it becomes obvious that the live molluscan fauna of Bahía la Choya is not randomly distributed, but that individual species are either fairly uniformly distributed across the tidal flat or else have their peak distribution in particular subenvironments. These subenvironments are defined by a number of parameters which include time of subaerial exposure, turbulence level, grain size, substrate consistency (hard-firm-soft) and stability, degree of reworking, depth of oxidation zone, temperature, salinity and food availability. Examples of apparently eurytopic species include *Chione californiensis* and *Nassarius iodes*, whilst stenotopic species include *Cerithidea mazatlanica* (tied to high intertidal and marsh areas), *Theodoxus luteofasciatus* (characteristic of gravel bars of the tidal channel and of exposures of Pleistocene hard substrate), and *Nassarius brunneostoma* (a species most abundant of inner flat firmgrounds). Some rare species not discussed in Figs 4–9 include *Melanipus mousleyi* and *Pedipes unisulcatus* which are restricted to salt marsh and *Donax gracilis*, occurring only in shallow subtidal environments. Relatively abundant, but living too deeply buried to be recovered by our sampling methods, is *Tagelus affinis*, a species typical of inner flat environments and in the tidal creeks within the salt marsh.

The live fauna of Bahía la Choya tidal flats can therefore be used to define various subenvironments, ranging from shallow subtidal, outer to mid flat, inner flat, salt marsh and channel (see also FLESA & FÜRSTICH this volume, for relation of molluscan communities to subenvironments).

A weak zonation can still be recognised in Fig. 12: For example, *Pteria sterna* and *Donax gracilis* are typical of shallow subtidal areas. The outer flat is dominated by *Cerithium stercusmuscarum* and mid to inner flat areas by *Lucina lanpra* and *Parvilucina mazatlanica*. *Cerithidea mazatlanica*, *Nassarius brunneostoma* and *Protothaca grata* are restricted to the innermost flat. Whilst *Cerithium stercusmuscarum*, *Cardita affinis* and *Pteria sterna* are clearly related to hard substrate, small lucinid shells are found in great abundance only in soft, sandy substrate. In Transect D (Fig. 13) no pattern is visible: Widespread, but patchily distributed Pleistocene rocks with patches of soft sediments inbetween cause a very patchy faunal distribution without any trends. This is well illustrated by the distribution of the gastropod *Cerithium stercusmuscarum*.

As a last example of faunal zonation along the four transects, the distribution of seven species of *Tellina* is shown in Fig. 14. Only data from Transects A and B are given. Distribution along Transect C is very similar to that of A and B, whilst in D the various species were not abundant enough to make any statements. Several species exhibit a clear preference for particular subenvironments. Thus, *T. amianta* is most abundant in shallow subtidal to outer flat areas as is *T. coani*. Most other *Tellina* occur from outer to mid flat; no species is found in inner flat areas.

These findings correspond to those of LINKE (1939), DORJES et al. (1969) and DORJES (1970) from North Sea tidal flats. These tidal flats are far more extensive and exhibit a greater range of substrates (fine-grained mud to shell gravel) than the Bahía la Choya tidal flat. The latter shows that even minor environmental changes are reflected by the species distribution of shelly remains.

LIVE-DEAD COMPARISONS

Figs 4–9 illustrate that the distribution patterns of many species from the taphocoenoses are close to those of the live fauna. This is surprising as the high tidal range of Bahía la Choya and resulting strong tidal currents suggests a high degree of sediment reworking and a high transport capability. The distribution of several species demonstrates that such transport indeed does take place, but appears to be significant in the tidal channel and on the inner flat firmground only. There it affects predominantly epifaunal species (*Cerithidea mazatlanica*, *Nassarius brunneostoma*). Because ebb flow is concentrated in the channel (in contrast to the incoming tide), a net seaward transport takes place.

A second mode of transport is the onshore transport of floating shells by the incoming tide, a phenomenon described in detail by SCHAFER (1953). Although we have observed floating shells transported over considerable distances, we regard this mode of transport as volumetrically insignificant in Bahía la Choya.

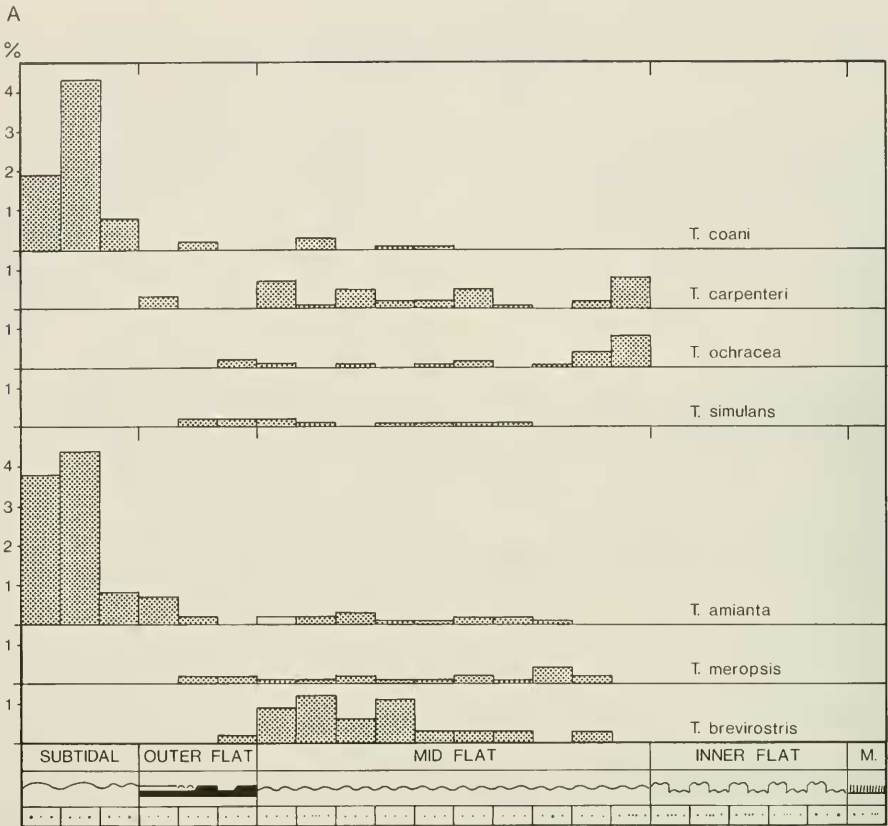


Fig. 14: Distribution of dead individuals of species of *Tellina* across the tidal flat. a: Transect A; b: Transect B. For key see Fig. 3.

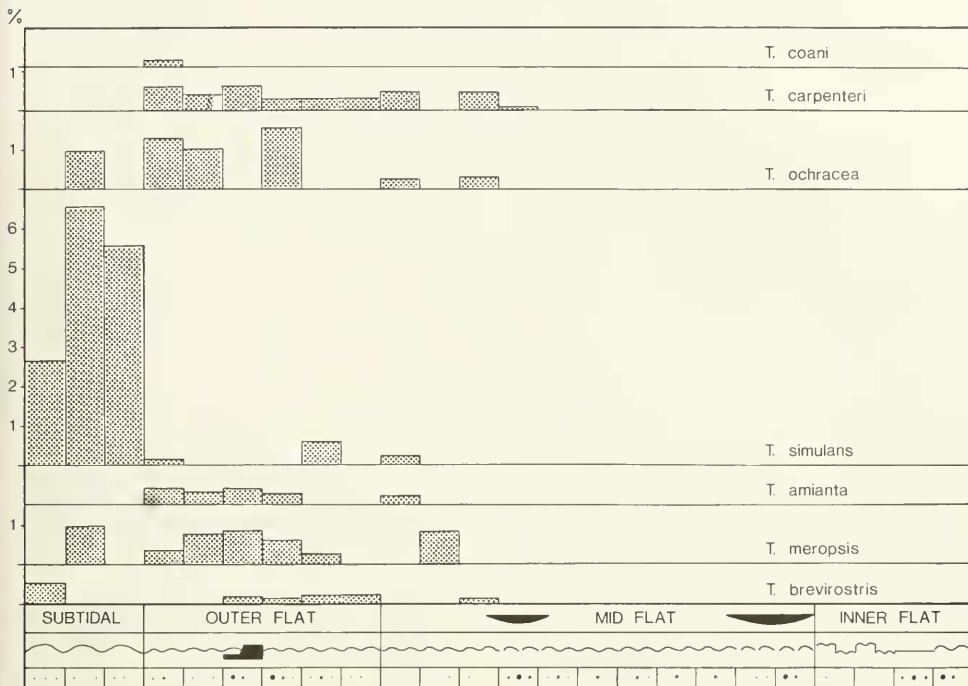
In contrast, a third mode of transport by biological agents is thought to be far more important, although affecting gastropod shells only. Hermit crab populations are high, particularly in the tidal channel. Counts in the channel of the outer mid flat showed that up to 52% of dead *Cerithium* shells and 36% of *Cerithidea* shells were inhabited by hermit crabs. As hermit crabs are known to migrate seasonally (e. g. FOTHERINGHAM 1975), faunal elements are likely to be transported across considerable distances this way, possibly in opposite direction to prevailing currents. It seems obvious that the discrepancies between live and dead distribution patterns of some species are, to a large extent, caused this way.

Comparing the diversity of live versus dead molluscs two features become apparent: (1) Dead molluscs are far more diverse than live ones (see also MACDONALD 1969, PETERSON 1977, POWELL et al. 1982); and (2) the diversity of dead shells decreases drastically at the boundary between mid and inner flat, whilst diversity of live molluscs remains relatively constant throughout (Fig. 3). Both features are related to the process of time-averaging. Fluctuations in larval settling and

minor environmental fluctuations will lead to changes in faunal composition resulting in a greater number of species in the taphocoenosis than in the live community (PETERSON 1977). However, with increasing harshness of the environment (in this case toward the high intertidal zone), only few species are able to successfully colonize the habitat. Fluctuations in faunal composition further seaward are not expected to be mirrored in the inner flat where temperature and salinity fluctuations, in combination with a very long subaerial exposure time, produce an environment unfavorable to most species. The set of species of this zone varies very little. Whilst pronounced time-averaging thus increases the diversity seaward, it does not have this effect on the taphocoenoses of the inner flat.

Additional agents that restrict the faunal diversity of the inner flat taphocoenosis are the low burial potential of faunal elements living on the firm substrate and the inability of many mollusc species to burrow into fairly cohesive, fine-grained sediment.

B



ZONATION OF DEAD MOLLUSCS

In Figs 4–14 many taxa of the taphocoenoses show a significant zonation across the tidal flat. Because of limited redistribution the zonation is less distinct than the zonation of live molluscs. For example, *Nassarius guaymasensis* occurs only in the shallow subtidal and outermost flat. *Theodoxus luteofasciatus* and *Cerithium stercusmuscarum* are characteristic of gravelly channel deposits and exposed rocky Pleistocene. The shallow subtidal mollusc fauna with *Pteria sterna*, *Laevicardium elenense* and *Donax gracilis* differs quite markedly from the tidal flat and the marsh fauna. Mixing which takes place on the tidal flat (e. g. by redistribution of *Cerithidea mazatlanica* and *Nassarius brunneostoma*) does not extend into the shallow subtidal where both forms are virtually absent. This implies that the subenvironments of the tidal flat can be defined by elements of the taphocoenoses.

Thus, despite tidal currents and biological activity information loss due to biostratigraphic processes is moderate. If diagenetic distortion of such taphocoenoses is small, benthic mollusc faunal elements can be expected to serve as useful indicators of ancient environments. The Bahia la Choya example also shows that pronounced time-averaging (see MELDAHL, 1987) does not significantly distort the faunal distribution pattern, but mainly influences species diversity. This suggests that in paleoecological analyses diversity values of time-averaged samples should not be compared to those of living communities (see also STAFF et al. 1986). In general, however, the pessimism about the usefulness of taphocoenoses and corresponding fossil assemblages for paleoecological and environmental analysis expressed by several authors (e. g. ANTIA 1977, CUMMINS et al. 1986, HOFFMAN 1982) cannot be shared (see also WARME 1969, WARME et al. 1976).

CONCLUSIONS

- (1) Live mollusc species of Bahia la Choya exhibit a zonation from the shallow subtidal to the high intertidal zone.
- (2) In many cases the distribution pattern of dead shells corresponds to that of live shells. Limited distortion of the original distribution pattern is caused by seaward transport

along the tidal channel and by biological transport caused by hermit crabs.

- (3) Faunal elements most affected by transport are the epifaunal inhabitants of the inner flat firmgrounds which provide a very low burial potential.

(4) Despite time-averaging and some degree of distortion, elements of the taphocoenoses characterize various subenvironments of Bahía la Choya.

(5) Even time-averaged samples record sufficient information for meaningful environmental analyses.

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